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BIOLOGY OF *ACMÆA TESTUDINALIS* MÜLLER.

M. A. WILLCOX.

Acmæa testudinalis Müller, the tortoise-shell limpet, as it is called by Forbes and Hanley, is the common limpet of our New England shores. It, together with its variety *alveus*, is the sole representative on this coast not only of its genus and family but of the entire group of the Docoglossa and by far the most convenient example of the suborder Diotocardia, which includes all the more primitive Gasteropods. It is abundant and accessible, it is easily kept alive in aquaria, and living as it often does in tide-pools, is conveniently observed under its natural conditions. But in spite of these facts it has never been made the subject of careful study.

I am at present engaged upon a paper which is intended to supply this lack and from which I excerpt the following biological notes.

Acmæa is a large genus whose eighty-four species are widely scattered over both northern and southern hemispheres. Representatives have been recorded not only from both eastern and western shores of all the great continents except Africa,[1] but from Australia, from New Zealand, and from many islands of the Atlantic and Pacific including some which are oceanic. The genus is at present arranged only tentatively. "More than any other shells, these must be studied with constant reference to not only habitat geographically, but *station* as well. For an exact knowledge of the group we must therefore wait until observations on the species are made with special reference to their modes of life and surroundings" (Pilsbry). It seems probable, moreover, that a careful comparative study of the different species might throw light upon various questions of geographical distribution. This statement of the final aim of the investigation may serve to explain the presence in these notes of material that might otherwise seem trivial. It is believed that nothing has been admitted which does not bear on the general question.

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[1] Two species only are as yet recorded from this continent: one from Natal and one from Cape Town.

Limpets are found on the entire New England coast and northward to the Arctic Ocean. Comparatively rare and local south of Cape Cod, they increase in numbers and in size as one passes northward until at Eastport, Maine, they are one of the most abundant of the littoral molluscs. They are found between tide-marks in pools and also in such shaded places as provide them at once with coolness and moisture. The vertical face of a rock heavily hung with dripping Fucus or the under surface of the larger beach pebbles are attractive spots. Although they are to be found occasionally where the water is at least slightly fouled by sewage, as in the estuary at Beverly, they are far more abundant in that which is clean and pure.

So far as reported they seem to reach their maximum size in the region of Eastport, which is bathed by the cool waters of the Arctic current. On the Massachusetts coast a limpet an inch long is a giant but at Eastport they not rarely reach a length of 32 mm. The first explanation of this fact which presents itself is of course that the cooler water presents the optimum temperature for these animals; this is not, however, the only possible explanation. The Arctic current is not only cooler but more equable in temperature than more southern waters. At Eastport the maximum yearly variation in temperature of the water is about 12° C. (32.5°–54° F.); at Boston it is nearly 23° C. (29°–70° F.).[1] Limpets living entirely below tide-mark would therefore enjoy comparatively equable temperature conditions at Eastport. This would not, however, be true for those living between tide-marks, for the annual variation in temperature of the air at Eastport is often as much as 35° C. (4°–67° F.) — 10° C., it may be, in a single month. Bathed twice a day by the water, exposed twice a day to the air, such individuals in spite of the comparatively cool places which they affect, would be exposed to conditions probably at least as variable as those of the Massachusetts waters. If now we examine their size with reference to their habitat, we find that the limpets of Eastport are large only when living at or near the low-water mark of spring tides so that they are rarely or never left uncovered by the sea, and that higher up on the beach the animals though no less abundant are of smaller size, no larger in fact than with us. We find also that in Massachusetts there is no marked difference in size between limpets which are continuously submerged and those which live between tide-marks. The conclusion is therefore forced upon us that size in these animals is correlated not necessarily with a low but with an equable temperature. The advantage of uniform thermal conditions was long ago pointed out by Möbius and Semper.

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[1] These figures are deduced from the records of the U. S. Weather Bureau at Eastport and Boston, for the years 1887–89, the only years during which observations of water temperature were made.

In the late autumn, limpets in the neighborhood of Boston either altogether disappear or become very scarce, reappearing in numbers in March or April. In Eastport, however, they remain near the shore for the entire year. Their disappearance from the Massachusetts coast is probably due to a retirement to deeper water; this is, I am told by Professor S. I. Smith, the practice among several of our littoral animals. Limpets will stand a good deal of cold; Miss Annie Sullivan, an observant and intelligent collector who is familiar with the animals at Eastport, tells me that she has revived them after ice had formed within the shell and found them apparently no worse for the experience. It seems very probable therefore, that when they withdraw in the autumn they go only a little below tide-mark, thus avoiding the very considerable daily variation in temperature to which they would often be subjected if they remained above the low-water line.

The distribution of limpets as given above is taken from Smith and Verrill's "Invertebrate Animals of Vineyard Sound," a work which was published nearly thirty-five years ago. I am not aware that any investigations have been undertaken since that time which would show whether it is still correct. Forbes and Hanley described this species in 1853 as having, at least in Great Britain and Ireland, a tendency to migrate southward and Forbes had already described its sudden appearance nearly twenty years before on the northern shore of the Isle of Man, where it is still to be found. In view of these facts it would be very interesting to learn whether it is moving southward on our own coast.

Distribution of the adult animal is probably effected not only through its own locomotion but also by the aid of tides and currents. On one occasion, though only on one, I found a limpet crawling back downward on the surface film like a fresh-water snail but I have not very infrequently found them clinging to floating pieces of the larger Floridiæ, upon which they feed. It will be remembered that Nacella and Helcioniscus live habitually upon the large fronds of Macrocystis. Occasional transportation of the adult by such means may not impossibly be a more effective factor in its distribution than the brief pelagic life of the young, which Boutan found in the case of *A. virginia* to be limited, at least in the waters of Roscoff, to a few days' duration.

Locomotion is almost exclusively effected by crawling over the substratum. Progress is exceedingly slow; the fastest crawling of which I have record was at the rate of about three inches per minute. This was in a tide pool where the animal was undisturbed and in natural conditions. Under such circumstances it often remains motionless for hours. In captivity it is not unusual to find one limpet crawling over another or adhering to its shell, although in such circumstances I have never observed either individual showing any recognition of the presence of another of its own kind.

In view of the well known homing habits of Patella and of the fact that I have found the same power possessed at least in a limited degree by animals so widely separated as *Fissurella barbadensis* Gmelin and *Siphonaria alternata* Say, I have made repeated attempts to satisfy myself of its existence in Acmæa. These attempts have, however, been unsuccessful. The difficulty lies in the character of the rocks of the New England coast, which are unsuited either to the formation of a sunken "scar" like that which indicates the home of Patella or of a discolored spot like that produced by Siphonaria. It is therefore impossible to locate with certainty the "home" of a limpet, which is the first step in determining whether or not it possesses the homing power. Dr. W. H. Dall, however, tells me that he has observed on the Pacific coast individuals of *Acmæa spectrum* Reese whose shell margins exactly corresponded to the irregularities of the soft rocks on which they live. Fisher notes that both this and other species of Acmæa are often found adhering to the shells of Lottia in which they have made shallow depressions. These observations furnish the strongest presumptive evidence that in some species, at all events, the homing power is present and render desirable the investigation of the question in *Acmæa testudinalis* under conditions more favorable than those afforded by the New England coast.

The food of limpets appears to be exclusively vegetable. A freshly taken specimen always has the digestive tract stuffed with a finely divided mass of unrecognizable material mingled with which are unicellular algæ and bits of the cortical cells of some of the larger ones. I have made no attempt to identify these organisms. Intermixed with this material are great numbers of tiny stones which probably, like those found in a bird's gizzard, aid in the comminution of the food. This is especially necessary in the limpet since for the greater part of their extent the walls of the alimentary tract are entirely devoid of muscles. These bits of stone are very likely, at least in large measure, fragments rasped off by the radula from the rocks together with the small algæ which cling to them. It has been suggested in regard to Patella that the bits of alga cortex are in like fashion detached, so to speak, by accident together with minute organisms both animal and vegetable, which live upon the alga and which constitute the real food of the limpet. Touching this suggestion I can only say that I have never found in any part of the alimentary tract of *Acmæa testudinalis* remains which could be interpreted as animal in nature and that I have found the animal apparently feeding upon large algæ which so far as one could see, were absolutely free from smaller organisms.

As to habits of feeding I have never been able to observe the act, but twice have, as I believe, interrupted it. In each case the seaweed to which the animal was attached bore a mark, due to the removal of the cortex, which served as a record of the movements of the snout during feeding. The head is evidently swept slowly from side to side while the animal *backs* gradually along the surface on which it is feeding, removing the food as it goes from a band whose width is equal to the diameter of its own mouth and whose length, disposed in a series of nearly parallel but connected arcs, is proportionate to the length of the feeding time. Removal of the tissue is effected by a licking motion of the odontophore or "tongue" with its superimposed radula but I have not been able to detect any independent motion of the radula although I have made an especial search for a "chain-saw movement" such as Huxley described in certain Heteropods, and Geddes claims to have seen "in live limpets turned over on their backs," and although there are in *Acmæa fragilis* muscles which seem adapted for the production of such a motion. I have also been unable to gather any evidence as to the way in which the individual teeth of the radula are used. Pilsbry has suggested that in Rhipidoglossa the rounded form of the subradular cartilage probably determines a greater activity of the median part of the radula and that this in turn accounts for the greater specialization of the teeth in that region.

Respiration is in general aquatic and the mantle no less than the gill serves as a respiratory organ, as is demonstrated by the disposition of the blood vessels and the course of the flow. Water passes in and out beneath the slightly raised shell and its character may very possibly be tested as among some Pelecypods by the minute tentacles which fringe the mantle. The shell is usually thus raised so long as the limpet is undisturbed though the slightest disturbance causes it to be tightly pressed against the supporting rock.

Atmospheric air may, however, under certain circumstances be respired. When the water in the aquarium has become unduly warm or otherwise deprived of a part of its air, it is a common sight to see the limpets about its edges with their bodies half out of the water, the shell raised to the highest point, and the head stretched forward so that the nuchal cavity may be as widely as possible opened to the air. Such a position seems explicable only on the theory that the animals are seeking to supplement the imperfect gaseous exchange permitted by the water by a true aërial respiration.

Limpets give evidence of the possession of only three special senses: sight, touch, and the temperature sense. If they are placed in water warmer than that to which they are accustomed, they betray their uneasiness by restless wandering about. Visual sensations appear to be limited to the perception of light and darkness. That light is objectionable only when associated with heat seems indicated by the following experiment: a limpet with the pebble to which it was affixed was removed from the shaded to the sunny part of a tide pool. The water, being 12 to 15 inches deep, effectually protected it from the heat of the sun and it showed no desire to move. When the pebble was placed, however, in water only an inch or two deep and so considerably warmer, the limpet exhibited lively discomfort and crawled at once toward the shade. I have assumed that the light-perceiving organs are the eyes but have taken no steps to prove it.

The sense of touch is possessed by the entire body surface though especially localized in the tentacles, both marginal and cephalic, which are richly provided with tactile (Flemming's) cells. The gill also, although without such cells, has an exquisite sensitiveness and from its exploratory movements while the animal is traveling, would seem to serve as an additional organ of touch.

Though the sexes in *Acmæa testudinalis* are distinct, the shells show no sexual differentiation, whether in size or in form; in the ripe animal, however, the sex can usually be determined by a difference in the tint in that part of the foot which immediately underlies the generative gland. The eggs when nearly ripe assume a tint much like that known among dry-goods merchants as "crushed strawberry," and the testis at the same period is of a golden brown. On the left side of the body the gland immediately overlies the foot and is perceptible through its tissue as a patch of dull reddish or of creamy brown bounded in the median plane by a sharp line corresponding to the plane where it abuts against the green nephridium.

The breeding season appears to be a long one; I have taken ripe limpets near Boston as early as the thirteenth of April and as late as the end of July. In Eastport they were still laying during the first week in September. In each place the generative season probably ends a little before the water reaches its maximum heat, which occurs at Eastport in September, at Boston in August. Thus all of a lot of specimens from Nahant in the middle of August had the generative glands empty and the same was true of a considerable part of those gathered at Eastport during the first few days of September. The eggs, which are about $\frac{1}{5}$ mm. in diameter are not dropped separately, as is said to be the case in Patella, but are imbedded in a layer of very thin mucus in which they lie one layer deep and at regular distances apart. The mucus is secreted not by a special gland but by the sole of the foot.

Fertilization is usually described as external. The only exception that I have been able to find to this statement is that of Fischer, who in 1863, asserted that he had found the ovaries of Patella filled with embryos already provided with the shell. Dr. Dall kindly informs me that he was following this authority when in 1879 he stated that the fertilization in Docoglossa is internal. His statement in turn seems to have been the authority for that made by Tryon in his Manual. While I am not prepared to assert that fertilization is internal I wish to record the following observation, which certainly points in that direction. About nightfall a male was observed caressing a female. Both shells were raised, that of the male overlapping the female and the heads were placed side by side, the male stroking the female with his tentacles. After a few passes he would turn as if he were going to leave her and then come back. The proceeding lasted for about half an hour, the female remaining quiescent with tentacles folded about her head. At the end of this time she moved forward, pressed the left side of the neck against the corresponding region in the male so that the openings of the two nuchal cavities were brought close together, and after remaining a moment or two in this position turned and walked away pushing with some difficulty between two other limpets neither of which paid her any other attention than a momentary touching with the tentacles. The nephridial papilla through which the generative products are extruded lies not on the left but on the right side of the nuchal cavity, but the ciliary current is outward on that side and inward on the left so that the position which I have described would seem on the whole better fitted than the reverse one for fertilization. On the other hand, however, it should be said that when the animals were killed twenty-four hours later, the ova of the female were unfertilized and no spermatozoa were observed in her nuchal cavity or nephridium. It should also be said that in two instances unfertilized eggs have been laid in my aquaria, but as the same thing sometimes occurs with moths when pairing is prevented, no deduction can be drawn from this fact.

The eggs, at least in the aquaria, are laid about nightfall and the trochosphere is developed in the course of the next day. I have made no attempt to watch the development. Growth must be rapid, as one finds at Nahant in September and early October large numbers obviously of the season's young, which are four or five mm. in length. Sexual maturity is probably acquired after the first winter, as I have taken ripe limpets in April which were under a cm. in length.

The only enemy of the limpet of which I have had any experience is the purple, *Purpura lapillus*. I have found occasional shells bored by this mollusc and in one instance was able to surprise it in the act.